

LIGHT DISTRIBUTION AND PHOTOSYNTHESIS OF *METROSIDEROS POLYMORPHA* FORESTS AT BOTH ENDS OF A NUTRIENT AND SUBSTRATE AGE GRADIENT IN HAWAII

S. CORDELL* AND G. GOLDSTEIN

Department of Botany, University of Hawaii, 3190 Maile Way, Honolulu, HI 96822, USA
E-mail: cordell@hawaii.edu

ABSTRACT. Patterns of light distribution, leaf area index (LAI), and canopy photosynthesis were studied in *Metrosideros polymorpha* forests at both ends of a nutrient and substrate age gradient in the Hawaiian Islands. The two sites differ in the age of the underlying volcanic substrate, and in being limited by nitrogen (N) in the young site (Thurston, Hawaii) and phosphorus (P) in the oldest site (Kokee, Kauai). Long-term fertilization with nitrogen (N), phosphorous (P) and N+P at both sites has resulted in leaf and canopy level changes. Light transmission through the canopy was lower in the N-addition plot than in the control plot. Increased LAI was observed at the N-amended plot, also suggesting greater light attenuation with increased N availability. While light intensity was not measured in the old site, LAI was much lower in the subcanopy and near ground levels than in the young site. Furthermore, the effects of nutrient amendments on LAI at the old site were not as large as those observed in the young site. Responses of net CO₂ assimilation (A) to fertilization were different at the young, and old sites. Instantaneous values of A remained constant across all plots at the young site, but significantly increased with nutrient amendments at the old site. In contrast, calculated values of canopy carbon gain (annual carbon gain * LAI) at the young site more than doubled with fertilization. The increase in canopy carbon gain at the young site was the result of larger leaves rather than higher photosynthetic rates. Variation on leaf area index and in light distribution was correlated to physiological and morphological traits of *M. polymorpha* dominated rain forests.

Key words: nutrient limitation, *Metrosideros polymorpha*, light environment, fertilization, LAI

INTRODUCTION

Resource limitations can affect growth, reproduction, and survival in plants. A resource is considered to be limiting if the addition of that resource will result in increased growth or fitness. Since properties of individual species can control the functioning of a group of co-occurring group of plants, community and ecosystem level characteristics will also be influenced by resource limitation (Vitousek 1982). To better understand ecosystem processes, it is necessary to understand how different resource limitations interact to affect plant growth and in turn ecosystem characteristics.

Nutrients and light availability are the most limiting resources in montane wet forests (Field & Mooney 1986, Chazdon 1988, Reich et al. 1992, Fetcher et al. 1994). Although light saturation for a single leaf occurs at a radiation far short of full sunlight, the arrangement and size of leaves within a canopy considerably alter the available light in a vertical distribution. In Hawaiian forests, nitrogen tends to be limiting in young soils, while phosphorus is limiting on older soils (Vitousek & Howarth 1991, Smith 1992, Herbert & Fownes 1995). A number of studies have reported correlations between some mea-

sure of photosynthetic capacity and total leaf nitrogen. This is based on the understanding that the photosynthetic machinery accounts for more than 50% of the nitrogen in a leaf and that photosynthesis is strongly affected by nitrogen availability (Field & Mooney 1986). Therefore, increased availability of nutrients for plant components coupled with increased photosynthetic capacity of leaves should result in increased plant growth. For example, in young substrate sites Vitousek et al. (1993) documented an increase in the diameter and height of *Metrosideros polymorpha* with the addition of nitrogen.

Because the coordinated responses of all photosynthetic processes, any environmental stress that reduces photosynthesis, such as nutrients, light, or water, will also inhibit leaf morphological traits and biochemical components (Lambers et al. 1998). Plants found in infertile sites tend to acclimate by producing long lived leaves that have a high leaf mass density (LMA), low foliar nitrogen concentration, and reduced photosynthetic capacity (Reich et al. 1992). High LMA, in turn, decreases the amount of leaf area available for light interception, thereby reducing the net relative growth rate of a forest stand. Recent evidence in Hawaiian ecosystems has shown strong trends in leaf size of *Metrosideros polymorpha* with substrate age and thus with in-

* Corresponding author.

creasing N availability (Geeske et al. 1994, Cordell et al. 1998).

Because *Metrosideros polymorpha* is the dominant canopy tree species found in Hawaiian rain forests it is expected that changes in leaf morphology and growth would affect the distribution of light through the canopy. Since light is a limiting resource that affects growth, survival and reproduction, any changes in the quality and quantity of the light regime may have an impact on the ecology and physiology of the canopy and understory species (Chazdon 1988, Fetcher et al. 1994).

Here, we investigate how nutrient availability affects the vertical distribution of light through the potential alteration of canopy structure by nutrient amendments. We will also assess the consequences for the efficiency of interception of light and how it translates into the canopy carbon balance.

MATERIALS AND METHODS

Description of Study Site

This study was performed in a very well defined and constrained age sequence of sites in the Hawaiian Islands. The sites differ in age of the underlying volcanic substrate, and in being demonstrably limited by N in young sites and P in the oldest site (Vitousek et al. 1993, Herbert & Fownes 1995). However, all are at the same elevation (1200 m), annual precipitation (2500 mm), topographic position, and all are dominated by the same species (Crews et al. 1995). Long-term (8–14 year) ongoing forest fertilization is in place at both the young and old extremes of the chronosequence.

Hawaii is an ideal place for this research; many of the factors that control plants and ecosystems can be kept constant, while others vary in wide but well-defined ways (Britten 1962, Vitousek et al. 1992). Climate varies widely in Hawaii as a function of elevation and exposure to the prevailing northeast trade winds, and climatic variation generally is predictable, continuous, and occurs on a very fine scale (Vitousek et al. 1992). Plant communities can be held constant to a striking extent. Hawaii is the most isolated archipelago on Earth, and the few natural colonists that have become established have radiated to occupy a broad range of environments (Carlquist 1980). The myrtaceous tree *Metrosideros polymorpha* Gaud. grows from sea level to 2500 m, from among the first woody colonists on young lava flows to the oldest substrates in the islands, and from <400 mm annual rainfall, to the wettest place on earth (Dawson & Stemmermann 1990). As the species name implies,

M. polymorpha exists in a number of forms including the pubescent varieties *incana* and *polymorpha* and the glabrous variety *glaberrima*. The pubescent varieties makes up ~95% of the *M. polymorpha* at the young site with *M. polymorpha* variety *glaberrima* making up the balance. *Metrosideros polymorpha* variety *glaberrima* is the sole variety of *Metrosideros* at the old site (Dawson & Stemmermann 1990). Parent material is also consistent; the chemistry of the volcanic material that makes up Hawaii reflects that of a stationary convective plume or “hot-spot” (Moore & Clague 1992), and is relatively constant on both short and long time scales (Wright & Helz 1987).

Complete factorial fertilizations have been carried out in the 300 and 4.1 million-year-old sites. The main treatments were N (100 kg/ha per year, half as urea and half as ammonium nitrate), P (100 kg/ha per year, triple superphosphate), and N plus P (100 kg N/ha per year + 100 kg P/ha per year). The field design consists of four blocks of eight 15 × 15 m plots in both the young (Thurston, Hawaii, hereafter, young) and old (Kokee, Kauai, hereafter, old) sites (TABLE 1). We conducted intensive measurements in one plot of each of four treatments at both the young and old extremes of the gradient (Control, N, P and N+P) yielding a total of 8 plots. Treatment plots were located in a very homogeneous forest stand with similar soil characteristics and slopes. Leaves from the upper canopy were accessed by scaffolding towers (1.6 m × 3.2 m) built to the height of the canopy (10–20 m). Towers were placed in the center of one plot per treatment. At least four canopy trees per plot were available from each tower. To address the problem of replication, sun leaves were shot down with a shotgun from three replicate plots per treatment (not accessible by towers). Morphological information was obtained from these leaves (area, weight, and LMA), and average values of all four replicate plots per treatment were used for calculations of whole leaf physiological and biochemical measurements. Photosynthetic gas exchange measurements were only obtained from plots with towers.

Leaf Area Index

Vertical leaf area index (LAI) was estimated nondestructively using a LAI-2000 plant canopy analyzer (LI-COR Inc., Lincoln, NE). Measurements were taken from within the upper canopy (13.5 m from ground), mid-canopy (6.5 m from ground), and below canopy (1.5 m from ground) at the young site and from 10, 5, and 1.5 m respectively from the old site. Time of day and orientation were held constant for each plot dur-

TABLE 1. Characteristics of study sites. Both sites are comprised of control plots, (C) (no added fertilizer) and plots which received additions of nitrogen (N), phosphorus (P), and a combined treatment containing nitrogen and phosphorus (N+P) (adapted from Vitousek, 1998).

Characteristic	Site	
	Thurston (young)	Kauai (old)
Volcano	Kilauea	Kauai
Substrate age (years)	300	4,100,000
Annual precipitation (mm)	2500	2500
Elevation (m)	~1200	~1200
Mean annual temperature (°C)	~16	~16
Treatments used in study	C,N,P,N+P	C,N,P,N+P
Date fertilization initiated	1985	1991
Limiting nutrients	N	P
Reference	Vitousek et al. 1993	Herbert and Fownes 1995

ing the study. Mid-canopy measurements were taken above a distinctive sub-canopy of tree ferns (*Cibotium* spp.).

Light Distribution

For the purpose of this study, we constructed 25 light sensors made of a light sensitive diode connected in parallel to a precision resistor. The sensor was connected to a coaxial cable and sealed in waterproof plastic shrink-wrap tubing to protect the wire cables. The voltage differential measured by the sensors were converted into photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) by calibrating the voltage difference against a quantum sensor (LI-COR Inc.) at different light intensities.

Light sensors were placed in the N fertilized and control plots and the young site in the following vertical gradient: 1) Within canopy—13.5 m from the ground, 2) above the sub-canopy tree fern (*Cibotium* spp.) layer—6.5 m from the ground, and 3) below the tree fern canopy—1.5 m from the ground. Sensors were attached to 1.6 m long PVC tubing and extended 1.3 m from canopy towers. Three diodes per height were attached to quantify the light from different aspects. In addition, a sensor was placed above the canopy (15 m from the ground). The diode sensors were attached at ground level to a data logger (CR-10, Campbell Scientific, Logan, UT), which recorded an average light measurement per minute.

Photosynthetic Gas Exchange

Net CO_2 assimilation was determined with a portable photosynthesis system (LI-6200; LI-COR Inc.). A portable light source was used to insure constant irradiance ($1600 \mu\text{mol m}^{-2} \text{s}^{-1}$) during measurements (Qbeam 6200; Quantum Devices Inc., WI). The light saturation point of

Metrosideros polymorpha is below $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Kitayama et al. 1997). Four fully expanded sun leaves (6–9 months old) were measured on each of four trees per treatment. Gas exchange was carried out between 0900 and 1500 hr to insure maximum rates. Measurements were repeated over a three-day period and during two different months of the year to account for seasonal variation (July and January). Values of annual carbon gain were obtained by averaging values of net assimilation of fully expanded sun leaves, and oldest non-necrotic leaves from the same branch leaves then scaling from $\mu\text{mol m}^{-2} \text{s}^{-1}$ to $\text{mol m}^{-2} \text{yr}^{-1}$. Canopy carbon gain is annual carbon gain * LAI (Kuppers 1994). Both estimates of carbon gain assume that all leaves receive the same amount of light, or are under light saturated conditions.

RESULTS

Light environment. Light penetration through the canopy was significantly lowered as a result of nitrogen fertilization. However, maximum values of photosynthetic photon flux density (PPFD) are similar between the control and nitrogen addition plots (FIGURE 1). This was especially evident in the mid-canopy above the tree fern layer.

LAI. Lai increased from above canopy to the forest floor in all plots (FIGURE 2). In the old site, LAI was significantly higher in the N+P addition plot than the control plot (FIGURE 2b). This was especially evident in the mid-canopy height. In the young, young site measurements of LAI were significantly higher in the N amended site than the control taken from both the mid-canopy and 1.5m from ground positions (FIGURE 2a). Mean values in the N amended plot were 2.5 versus 0.9 in the control plot at the mid-canopy level, and at the 1.5 m from ground

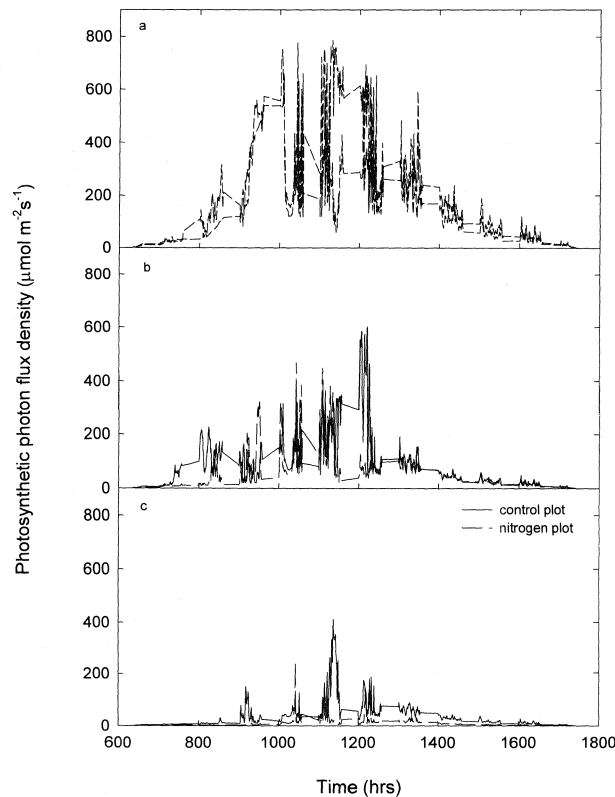


FIGURE 1. Diurnal variation in photosynthetic photon flux density (PPFD) in a *Metrosideros polymorpha* dominated rain forest at: **a**, canopy level (13.5 m); **b**, mid-canopy (6.5 m); and **c**, below the tree fern canopy (1.5 m).

level, 5.0 and 2.5 respectively (FIGURE 2a). Because of a very obvious N fertilizer effect on the sub-canopy tree fern layer (pers. obs.), comparisons of LAI of *Metrosideros polymorpha* appear to be most valid at the mid-canopy level (above tree fern layer).

Carbon assimilation. Net CO_2 assimilation (A) of *Metrosideros polymorpha* leaves was different for the young, young site, and the older, old site, and was differentially affected by fertilization at both sites (TABLE 2). At the young site instantaneous values of A and calculated values of annual carbon gain were essentially constant, regardless of nutrient additions, whereas at the old site instantaneous values of A and calculated values of annual carbon gain increased significantly in the N, P and N+P addition plots. However, calculated values of canopy carbon gain show a more than two-fold increase in both the young and old sites in the fertilized versus, non-fertilized plots (TABLE 2).

DISCUSSION

The results of this study suggest that there are striking contrasts between the consequences of N additions in young ecosystems and those of P additions in old systems. Our results show lower light penetration through the canopy in the N-addition plot than the control at the young site. Increased values of LAI were measured in the N-amended plot, also indicating greater light attenuation with increased N availability. However, in terms of peak values of photosynthetic active radiation (PPFD), leaves at the bottom of the trees experienced irradiances similar to those measured in the mid-canopy level, and are similar between the control and nitrogen addition plots. This can be attributed to the frequent occurrence of sunflecks through the canopy. Although these sunflecks may occur very briefly, their contribution to the total quantum flux can be substantial, providing up to 85% of the total daily photons received (Percy 1987, Chazdon 1988). *Metrosideros polymorpha* forests do not

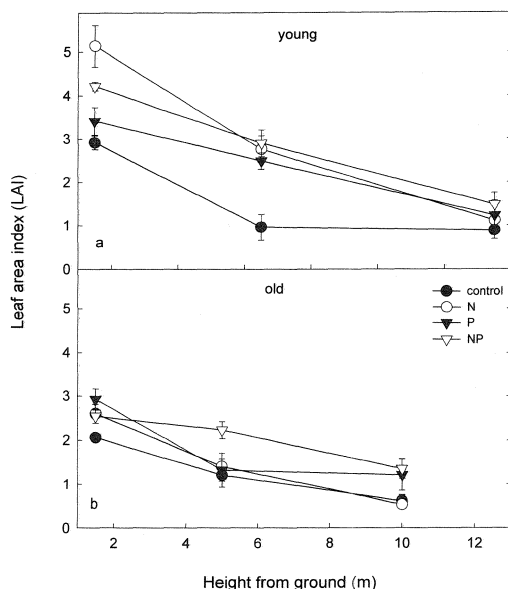


FIGURE 2. Leaf area index (LAI) at three different heights within *Metrosideros polymorpha* dominated forests. **a.** young site. **b.** old site. Each point is a mean of nine measurements from each treatment plot \pm SE.

typically form a closed canopy, and the crowns of *M. polymorpha* are not evenly or uniformly shaped (pers. obs.). It has been speculated that light availability is higher in Hawaiian forests than those in similar mainland tropical habitats (Pearcy 1983, Chazdon & Fetcher 1984, Chazdon et al. 1996, Pattison et al. 1998), and that because of the low diversity and disharmonic flora in the Hawaiian Islands, there is less selective pressure to compete for light resources (Pattison et al. 1998). Results from this study

showed a pronounced decrease in light levels from the canopy to the forest floor. As mentioned above, peak values of PPFD were consistently higher than $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ between 0900 and 1230 in the mid-canopy, and 1000 and 1200 hours in the low canopy. Because the light saturation point of *M. polymorpha* is low ($250 \mu\text{mol m}^{-2} \text{s}^{-1}$; Kitayama et al. 1997), understory *M. polymorpha* leaves experience light saturation for considerable periods throughout the morning when photosynthesis is most active. This is contrary to most studies of understory plants which show that carbon assimilation is strongly dependent on sunflecks, which may account for less than 20 minutes of adequate photosynthetic light per day, with the remainder of available light being diffuse ($10\text{--}20 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Pearcy 1987). While not conclusive, this data suggests that the low species diversity among canopy and understory species relative to other tropical systems and the effects of canopy structure and distribution, leads to less light interception in Hawaiian rain forests.

While the light environment was not studied in the old site, values of LAI were much lower in the mid-canopy and near ground levels than values of LAI from the young site. Furthermore, the effect of nutrient amendments at the old site was not nearly as substantial as shown in the young site.

Decreased light attenuation appears to be coupled with increased nutrient availability at the young site. While the effect was most obvious in the N-amended plot, significant differences of increased LAI values associated with P, and N+P additions at the same site were observed. This result is especially interesting considering that foliar N concentrations in the young site do not show a substantial increase upon removal of

TABLE 2. Photosynthetic characteristics, annual carbon gain, and canopy parameters of Hawaiian *Metrosideros polymorpha* from fertilized and unfertilized treatment plots at the young and old sites. N, nitrogen; P, phosphorus. Net CO_2 assimilation is the weighted average value of maximum rates of fully expanded and the oldest non-necrotic leaves on the same branch. Estimates of canopy carbon balance = Annual carbon gain \times leaf area index (LAI) (Kuppers 1994). This estimate assumes each leaf is under light saturated conditions.

Site	Treatment	Net assimilation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Annual carbon gain ($\text{mol m}^{-2} \text{yr}^{-1}$)	LAI	Canopy carbon ($\text{mol m}^{-2} \text{yr}^{-1}$)
Young (300 years)	Control	6.5	20.4	0.96	19.6
	N	6.4	20.1	2.8	55.5
	P	6.1	19.1	2.5	47.6
	N+P	6.1	19.3	2.9	56.1
Old (4.1 million years)	Control	3.6	11.3	1.2	13.7
	N	6.2	19.5	1.4	27.4
	P	5.9	18.7	1.3	24.8
	N+P	5.3	16.7	2.2	36.7

the limitation. While foliar N concentrations do not respond to N additions at the young site, primary productivity has increased as a result of fertilization (Vitousek et al. 1993).

Analysis of canopy carbon gain from this study provides further evidence of increased productivity associated with nutrient amendments. While instantaneous rates of *A* remain essentially constant despite fertilization at the young site, canopy carbon gain increases by more than 50% upon fertilization. This suggests that increased productivity directly correlates with increased leaf size upon fertilization. At the young site leaf size almost doubled with N additions [4.8 cm² (control) to 7.4 cm² (N-addition)] (results not shown). Larger leaf size increases surface area, which directly increases light interception and CO₂ capture. Rates of net CO₂ assimilation on a whole leaf basis are increased, and the overall effect is an increase in total biomass. Interestingly, additions of P, and N+P also reveal substantial increases in canopy carbon gain, despite P being a non-limiting nutrient at the young site. However, leaf size also significantly increased upon addition of P at this site, again directly correlating with increased productivity and decreased light penetration. The influence of crown structure on the variability in measured light conditions supports the conclusion of Chazdon et al. (1988), where *Piper* spp. from different environments were compared. In their study, variation in light within different habitats was strongly associated by leaf positions and leaf angles within crowns. While these canopy parameters were not analyzed in this study, variations in crown structure influenced by changes in leaf size were observed. In a complimentary study, using the same *Piper* spp. Walters and Field (1987) noted that despite large variation in the light environment, *Piper* had very similar photosynthetic characteristics. They conclude that differences in growth form, branching pattern, biomass allocation, leaf size, and leaf turnover contribute to the noted variation in the light environment.

Variation in instantaneous values of net CO₂ assimilation (*A*), annual carbon gain and canopy carbon gain at the old site were strongly affected by fertilization. Additions of N, P and N+P significantly increased both measured instantaneous values of *A* and calculated carbon gain at this site, despite small changes in measured LAI across plots. Unlike large changes in leaf size associated with fertilization at the young site, leaf size at the old site remained essentially constant across all plots (results not shown). Furthermore, foliar concentrations of nutrients, particularly P, significantly increased with fertilization at the old site (Vitousek 1998). Therefore,

it appears that increased nutrient availability at the older old site led to an increase in the photosynthetic rate per unit leaf surface area, with no concomitant change in leaf size.

In summary, these data point to a correlation between physiological and morphological traits and environmental conditions. Furthermore, leaf level responses associated with increases in primary productivity suggest that differential allocation processes are driven by morphological or biochemical acclimation responses. These data demonstrate how variation in leaf area index and light distribution correlates with physiological and morphological traits of *Metrosideros polymorpha* in Hawaiian rain forests.

ACKNOWLEDGMENTS

The authors wish to acknowledge Heather Jeppesen, Ryan Okano, and Randy Senock for their invaluable technical support, and tireless assistance with tower building and data collection, and Debbie Carino, Randy Amiscaray, and Stephanie Loo for initiating, constructing, and monitoring the light sensor project. This research was supported by a USDA grant (#941156365) to P. Vitousek and Guillermo Goldstein, and a NSF Doctoral Dissertation Improvement Grant.

LITERATURE CITED

- Britten, E.J. 1962. Hawaii as a natural laboratory for research on climate and plant response. *Pacific Sci.* 16: 160–169.
- Carlquist, S.C. 1980. Hawaii, A Natural History. Pacific Tropical Botanical Garden, Lawai, Hawaii.
- Chazdon, R.L. 1988. Sunflecks and their importance to forest understory plants. *Advances Ecol. Res.* 18: 1–63.
- , R. Pearcy, R. Lee and N. Fetcher. 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. Pp. 5–53 in S. Mulkey, R. Chazdon and A. Smith, eds. *Tropical Plant Ecophysiology*. Chapman and Hall, New York.
- Cordell, S., G. Goldstein, D. Mueller-Mombois, D. Webb and P.M. Vitousek. 1998. Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia* 113: 118–196.
- Crews, T.E., K. Kitayama, J. Fownes, D. Herbert, D. Mueller-Dombois, R.H. Riley and P.M. Vitousek. 1995. Changes in soil phosphorus and ecosystem dynamics across a long soil chronosequence in Hawaii. *Ecology* 76: 1407–1424.
- Dawson, J.W. and R.L. Stemmermann. 1990. *Metrosideros Banks ex. Gaertn.* Pp. 964–970 in W.L. Wagner, D.H. Herbst and S.H. Sohmer, eds. *Manual of the Flowering Plants of Hawaii*. Bernice P. Bishop Museum, Honolulu, Hawaii, USA.

- Fletcher, N., S.F. Oberbauer and R.L. Chazdon. 1994. Physiological ecology of plants at La Selva. pp. 128–141 in L. McDade, K.S. Bawa, H. Hespeler and G. Hartshorn, eds. *La Selva: Ecology and Natural History of a Neotropical Rainforest*. University of Chicago Press, Chicago.
- Field, C. and H.A. Mooney. 1986. The photosynthesis-nitrogen relationships in wild plants. Pp. 25–55 in T.J. Givinish, ed. *On the Economy of Plant Form and Function*. Cambridge University Press, Cambridge.
- Geeske, J., G. Aplet and P.M. Vitousek. 1994. Leaf Morphology along environmental gradients in Hawaiian *Metrosideros polymorpha*. *Biotropica* 26: 17–22.
- Herbert, D. and J Fownes. 1995. Phosphorus limitation of forest leaf area and net primary productivity on a weathered tropical soil. *Biogeochemistry* 29: 223–235.
- Kitayama, K., R. Pattison, S. Cordell, D. Webb and D. Mueller-Dombois. 1997. Ecological and genetic implications of foliar polymorphism in *Metrosideros polymorpha* Gaud. (Myrtaceae) in a habitat matrix on Mauna Loa, Hawaii. *Ann. Bot.* 80: 491–497.
- Kuppers, M. 1994. Canopy Gaps: Competitive Light Interception and Economic Space-Filling—A matter of Whole Plant Allocation. Pp. 111–144 in M. Caldwell and R. Pearcy, eds. *Exploitation of Environmental Heterogeneity by Plants: Ecophysiological processes above- and below ground*. Academic Press, San Diego.
- Labbers, H., F.S. Chapin III and T.L. Pons, eds. 1998. *Plant Physiological Ecology*. Springer, New York.
- Moore, J. and D. Clague. 1992. Volcano growth and evolution of the island of Hawaii. *Geol. Soc. Amer. Bull.* 104: 1471–1484.
- Pattison, R., G. Goldstein and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rain forest species. *Oecologia* 118: 449–459.
- Pearcy, R. 1983. The light environment and growth of C_3 and C_4 species in the understory of a Hawaiian forest. *Oecologia* 58: 26–32.
- . 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap, and understory microenvironments. *Funct. Ecol.* 1: 169–178.
- Reich, P.B., M.B. Walters and D.S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62: 365–392.
- Smith, V.H. 1992. Effects of nitrogen: phosphorus supply ratios on nitrogen fixation in agricultural and pastoral systems. *Biogeochemistry* 23: 197–215.
- Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. *Amer. Nat.* 119: 553–572.
- . 1998. Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. *Ecosystems* 1: 401–407.
- Vitousek, P.M., G. Aplet, D. Turner and J.J. Lockwood. 1992. The Mauna Loa environmental matrix: foliar and soil nutrients. *Oecologia* 89: 372–382.
- and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13: 87–115.
- Vitousek, P.M., L.R. Walker, L.D. Whiteaker and P.A. Matson. 1993. Nutrient limitation to plant growth during primary succession in Hawaii Volcanoes National park. *Biogeochemistry* 23: 197–215.
- Walters, M. and C. Field. 1987. Photosynthetic light acclimation in two rainforest *Piper* species with different ecological amplitudes. *Oecologia* 72: 449–456.
- Wright, T.L. and R.T. Helz. 1987. Recent advances in Hawaiian petrology and geochemistry. In R.W. Decker, T.L. Wright and P.H. Stauffer, eds. *Volcanism in Hawaii*. 1350. U.S. Geological Survey Professional Paper, Washington, D.C.